Predicting Trophic Interactions and Habitat Utilization in the California Current Ecosystem

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LONG-TERM GOALS

While specifically focusing on trophic interactions affecting habitat utilization and foraging pattern of California sea lions (CSL) in the California Current Large Marine Ecosystem (CCLME), the long-term goal of our modeling approach is to better understand and characterize biological "hotspots" (i.e., the aggregation of multiple marine organisms over multiple trophic levels) off the U.S. west coast and in other regions where similar fully-coupled ecosystem models may be implemented. As such, our research represents a major step towards a predictive model that can provide fundamental knowledge about: (1) the spatial and temporal distribution of key marine organisms over multiple trophic levels, and (2) natural and anthropogenic variability in ecosystem structure and trophic interactions

OBJECTIVES

The main research objective is to quantify habitat utilization and trophic interactions in the CCLME by considering patterns of covariability between environmental variables (e.g., temperature, primary production) and foraging patterns and success of middle (forage fish) and higher (sea lions) trophic level organisms. Since our numerical experiments are designed to isolate patterns of variability on seasonal to interannual timescales during "normal" and "extreme" years, we focus our analysis on identifying shifts in habitat utilization (e.g., shelf vs. offshore foraging) in the CCLME. We will also explore which features and environmental properties control foraging success in different sub-regions of the CCLME (e.g., onset and duration of upwelling season on the shelf, eddy variability).

APPROACH

Our fully-coupled ecosystem modeling framework consists of a lower trophic level ecosystem model (NEMURO) embedded in a regional ocean circulation model (ROMS), and both coupled with a multi-species individual-based model (IBM) for forage fish and higher trophic level species. The IBM for forage fish focuses on two coastal pelagic species (sardines and anchovies), with growth based on bioenergetics, temperature and prey generated from the ROMS and NEMURO models. The IBM for higher trophic level predatory species focuses on the implementation of a bioenergetics and behavior model for CSL by using available data on their foraging patterns and diet in the CCLME. The numerical experiments with the fully-coupled ecosystem modeling framework are designed to identify

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patterns of trophic interactions and habitat utilization on various timescales, including periods of extreme variability such as El Niño or La Niña events. Our team includes expertise in areas including climate modeling in upwelling regions (Enrique Curchitser), physical-biological modeling in the CCLME (Jerome Fiechter and Christopher Edwards), data assimilative methods (Andrew Moore), forage fish ecology (Kenneth Rose), and pinniped ecology (Daniel Costa). The team also includes a postdoctoral research associate (Luis Huckstadt) who will develop the bioenergetics and behavior components for the CSL IBM under the supervision of Costa.

WORK COMPLETED

We completed the first year of the project, and our progress to date is on track with respect to the proposed milestones for Year 1. As of 1 September 2013, we have achieved the following main tasks: (1) completion of baseline run with coupled ROMS-NEMURO-Fish IBM model, (2) development of bioenergetics model for male CSL, and (3) implementation of CSL IBM in the ecosystem model.

A. Baseline 50-year run of ROMS-NEMURO-IBM model
We have implemented ROMS-NEMURO-IBM model for the CCLME region, and generated a 50-year (1959-2009) baseline solution using the following configuration:

 ROMS: The model domain ranges from 30°N to 48°N and 116°W to 134°W, with a horizontal grid resolution is 1/10° (ca. 10 km) and a vertical resolution of 42 terrain-following levels. Open boundary conditions and surface atmospheric forcing for ROMS are derived respectively from the Simple Ocean Data Assimilation (SODA) reanalysis and from the datasets for Common Ocean-Ice Reference Experiments (CORE2). SODA and CORE2 both encompass the period 1959-2009, which allows us to run a realistic, 50-year forward integration of the fully coupled ecosystem model.

 NEMURO: The 11-component NEMURO model was specifically developed and parameterized for the North Pacific, and includes three limiting macro-nutrients (nitrate, ammonium and silicic acid), two phytoplankton size-classes (nanophytoplankton and diatoms), three zooplankton size-classes (micro-, meso-, and predatory zooplankton), and three detritus pools (dissolved and particulate organic nitrogen and particulate silica). NEMURO is coupled to ROMS by solving a transport equation in ROMS for each NEMURO component at every time step.

 Fish and CSL IBM: To facilitate interactions between the IBM and ROMS and NEMURO, the fish and CSL individuals are tracked in continuous (Lagrangian) space within the ROMS grid with hourly updates of their positions (i.e., grid cell location). Since locations are updated hourly, fish and CSL attributes determined by environmental conditions (e.g., growth, behavior) are updated at the same frequency. For male CSL, hourly consumption and energy requirements are calculated based on a bioenergetics model recently developed as part of this project first year effort (see section below). For now, CSL are moved horizontally using a random walk approach with foraging trip and haul out durations based on energy requirements to maintain a constant weight. More complex behavior based on actual CSL tracks will be implemented during the second year of this project.

B. California Sea Lion Bioenergetics Model
We built a mechanistic dynamic bioenergetics model for male CSL, which separates the energy demands of an animal between two main components: production (somatic and reproductive growth) and maintenance (resting metabolism, activity and work, cost of digestion, etc.). Since the costs

associated with reproductive growth can be neglected for male mammals, we can represent our model as: "Production = Consumption – Metabolism – Waste".

Production: Our model calculates the desired daily growth in length of CSL based on the length-age relationship (von Bertalanffy). This desired increase in length is easily converted to mass using an allometric relationship (obtained as part of this modeling effort based on field data on male CSL from central California). For simplicity, any changes in body mass are ultimately due to changes in the fat and protein fractions, and excess energy is allocated to depot fat. Depending on the daily balance between required energy and energy acquired, three different scenarios are considered: optimal growth, sub-optimal growth, and negative growth. The model dynamically tracks the changes in the protein and fat components, and assumes loss of the individual when the fat component reaches 5% body mass.

Consumption: The model calculates the energy consumption of CSL on a daily basis. Our model estimates daily food consumption for CSL based on its relationship with body mass calculated for animals in captivity. The daily diet of CSL can be composed of one, or a desired combination of up to four prey species (anchovy, sardine, market squid and mackerel). These four prey items were included in our model based on their importance in the diet of CSL off California, as well as the availability of information on their specific energetic density and assimilation efficiency for the species.

Metabolism: Resting metabolic rate is calculated based on daily mass only, while at-sea, field metabolic rate is modeled as a function of the total distance traveled by the individual sea lion in one day. The amphibian nature of CSL dictates its metabolic needs. While hauling out on land, CSL does not acquire food and has no metabolic costs associated with movement or digestion. Hence, the model still calculates a daily metabolic cost associated with being on land (when CSL are often resting or sleeping) by adding a multiplier of 1.2 times the resting rate.

RESULTS

A. Baseline 50-year run of ROMS-NEMURO-IBM model
The main accomplishment in running a 50-year integration of the fully coupled ecosystem model was to establish a baseline for normal vs. "extreme" conditions, and to identify how environmental variability propagates up the trophic levels. Results from ROMS and NEMURO indicate that the model is able to reproduce physical and biological variability associated with the El Niño Southern Oscillation (ENSO) in the CCLME (Fig. 1). This was an important point to demonstrate since shifts in CSL foraging patterns from inshore to offshore were observed during warmer and less productive conditions off California. It was also important to establish that anomalous conditions in the physical fields (e.g. temperature) translated into anomalous conditions in the biological fields (i.e., primary and secondary production) as well. We have also found that the lower trophic level ecosystem anomalies affect sardine and anchovy population dynamics via early life survival and condition at recruitment.
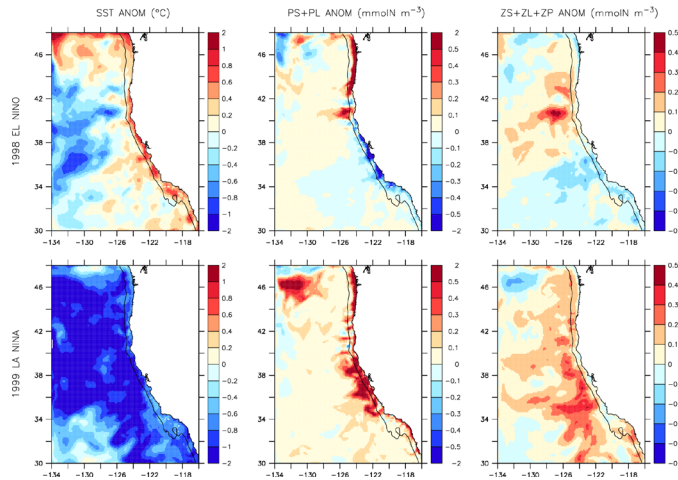
Figure 1. Output from ROMS and NEMURO illustrating extreme conditions associated with the 1998 El Nino (top) and 1999 La Nina (bottom). From left-to-right: annual sea surface temperature, phytoplankton, and zooplankton anomalies with respect to their 1959-2009 means. The results show that the coupled ecosystem model is capable of reproducing the significant anomalies associated with ENSO variability in the CCLME (i.e., high (low) temperatures and low (high) production during El Nino (La Nina)).

Since sea lions respond to changes in sardine and anchovy abundance via consumption to meet their bioenergetics requirements, we expect that the model will show different foraging patterns and/or growth conditions during anomalous years, such as ENSO events. Identifying changes in feeding strategy (e.g., location, diet) during normal and "extreme" years will be the main task for the second year of the project. So far, we tested the implementation of the CSL bioenergetics in the IBM by running a simple simulation with ten sea lion individuals and a random walk foraging behavior in the vicinity of Monterey Bay, California. The duration of foraging trips and haul out periods was dynamically adjusted based on the sea lion maintaining their initial weight, as well as protein and fat contents. Preliminary results from the fully coupled ecosystem model show that, even with a simple random behavior, CSL individuals are able to prey on sardine and anchovy individuals. The results also show that, as expected, CSL feed primarily on anchovy (i.e., the more coastal species), but that there is a seasonal component to their diet, with relative sardine consumption increasing during spring and early summer (Fig. 2).

B. California Sea Lion Bioenergetics Model
The main accomplishment in developing the bioenergetics model for male CSL was the ability to test its robustness to parameterization using actual sea lion foraging tracks from the Central California region. The results suggest that daily food intake derived from laboratory experiments is not sufficient to sustain metabolism given typical at sea and hauled out behavior for male CSL (Fig. 3, right panels; red, blue, and green curves). In fact, the bioenergetics model indicates that daily food intake must be increased by ca. 30% above laboratory values to achieve stable weight and body protein and fat contents. Establish this result was important, as it will help understand response curves from the fully coupled ecosystem model when CSL daily food consumption is dynamically influenced by the ability to locate sardine and anchovy prey individuals. Furthermore, it will ensure that the average daily consumption requirements imposed in the CSL IBM are consistent with actual sea lion foraging data for the region considered.
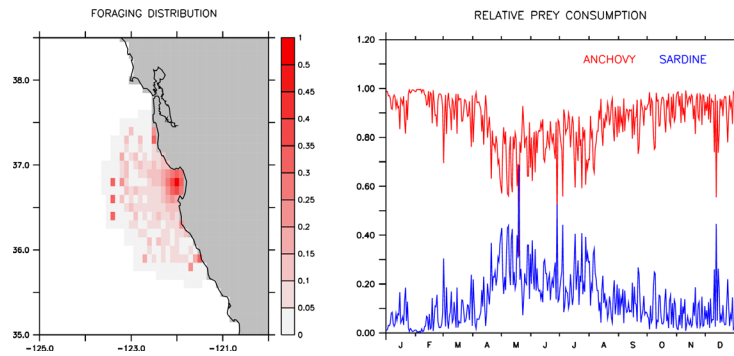
Figure 2. Output from the fish and CSL IBMs showing mean foraging patterns (left) and daily relative consumption of sardine and anchovy (right) based on ten male sea lion individuals in the vicinity of Monterey Bay. CSL foraging duration is based on maintaining energy requirements from bioenergetics model.
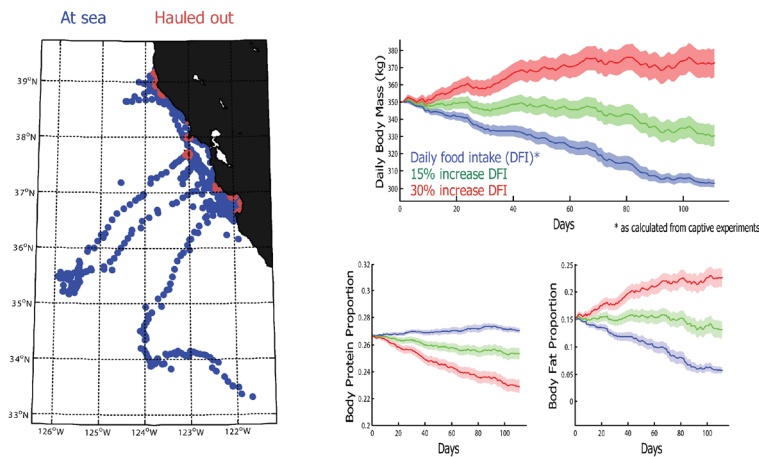
Figure 3. Simulated changes in body mass, fat and protein content of male adult CSL from the bioenergetics model using activity patterns from satellite tracking data (left panel). Three scenarios were considered (right panels): daily food intake (DFI) from experiments with captive CSL (blue), and DFI increase by 15% (green) and 30% (red). Solid lines represent mean values and shaded areas indicate standard deviation obtained from bootstrapping (10,000 samples).

By adding uncertainty to the bioenergetics model parameters and CSL mass-length relationship (either from ranges reported in the literature or Bayesian inference), we were able to obtain standard deviation estimates around the mean weight, protein, and fat values using a bootstrapping method. The results suggests that the response curves from the bioenergetics model are relatively robust to uncertainty in parameterization and mass-length relationship, with standard deviations typically less than 5% of the mean values (Fig. 3, right panels; shaded areas around solid curves). The relative robustness to uncertainty in bioenergetics model parameterization was an important result to demonstrate, as we try to identify variability in foraging patterns and success from bottom-up controls in the fully coupled ecosystem model.

IMPACT/APPLICATIONS

While focusing on the development of an individual-based model for California sea lions and its incorporation into a fully-coupled ecosystem model, the proposed research will pave the way for building a more comprehensive fully-coupled ecosystem model framework that can account for multiple species across several trophic levels. Since other apex predators utilize the CCLME as a transit region (e.g., northern elephant seals, whales) or feeding ground (e.g., tunas, sharks), understanding how variability in environmental conditions affect habitat utilization of one particular species may shed light on which physical and biological processes control the distribution of other key marine organisms over a range of spatial and temporal scales. In addition, this information will eventually lead to characterizing biological "hotspots" (i.e., the aggregation of multiple marine organisms over multiple trophic levels) in the CCLME, or other regions where similar fully-coupled ecosystem models may be implemented (e.g., Southern Ocean).

A main advantage in using model output to diagnose the occurrence and persistence of biological hotspots is the access to all physical and biological variables (e.g., water column temperature, primary production, growth rates, behavioral cues) at multiple temporal and spatial scales needed to characterize which particular environmental conditions and which particular foraging strategies were conducive to aggregation over multiple trophic levels. Once these fundamental mechanisms are better understood, our proposed ecosystem model framework could for instance be used to predict how climate variability may impact suitable habitat distributions in the CCLME or other regions of the world oceans.

RELATED PROJECTS

PI Fiechter and co-PIs Edwards and Moore are collaborating on an NSF-funded project (PI Moore; award dates: 04/01/2011-03/31/2014) entitled: "Variability of the California Current System Derived from 4D-Var Circulation Estimates". Our current ONR project will benefit from the 4D-Var circulation estimates to improve the accuracy with which the integrated ecosystem model reproduces environmental variability in the California Current (e.g., temperature, phytoplankton). The 4D-Var work will also inform our proposed research on which aspects of seasonal and interannual variability may not be adequately reproduced by ROMS without use of data assimilation.